REPRODUCTIVE BIOLOGY OF THE HANUMAN LANGUR *PRESBYTIS ENTELLUS* IN JODHPUR, WESTERN INDIA[1]

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(With four text-figures)

Introduction

The Hanuman langur *Presbytis entellus* Dufresene 1797 (Primates: Cercopithecidae), lives in a variety of habitats in India, which range from the snow-clad peaks of the Himalaya (up to 3660 m) in the north to deciduous forests in the south, parts of the Great Indian Desert in the west and to the rain forests in the east (Roonwal and Mohnot 1977).

Although a large number of field studies have been carried out on the behaviour and ecology of Hanuman langurs in different ecozones for the last two decades (Laws and Vonder Har Laws 1984 and references therein, Newton 1986, Sommer 1987), detailed information on the reproductive biology is not available (Harley 1985).

Adult male replacements, social changes and infant killings were frequently reported in this species (Sugiyama 1965, Mohnot 1971, Hrdy 1977, Makwana 1980, Sommer 1987, Agoramoorthy and Mohnot 1988, Agoramoorthy *et al.* 1988) but controversies still exist over different hypotheses in connection with frequency, cause and function of langur infanticide (Hrdy 1974, Curtin and Dolhinow 1978, Boggess 1979, 1984).

The collection of quantitative longitudinal reproductive and troop demographic data thus became important in order to test hypotheses concerning the functional aspect of infanticide. This paper describes the female reproductive parameters and troop development in three one-male bisexual troops of Hanuman langur. This study was carried out from December 1982 to September 1985 around Jodhpur in western India.

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Study Area

Jodhpur city (26°19' N, 73° 8' E, elevation 241 m) lies at the eastern fringe of the Great Indian Desert in western India. The study area named Kailana-Bijolai is located about 8 km west of Jodhpur, which has undulating hillocks in a semi-arid environment, where *Euphorbia caudicifolia* and *Acacia senegal* are predominant.

The climate of Jodhpur and its vicinity is characterised by uncertain and variable rains and extremes of temperature (Mohnot 1974). The lowest temperature during the study was 1° C (21 Feb. 1984) and the highest was 44.7° C (28 May 1984). Rain usually occurs in summer monsoons during July to September and the mean annual rainfall during 1983-84 was 360 mm.

Material and Methods

Langur troops: About 1300 langurs organized in 28 one-male bisexual troops (66.7%), one multi-male troop (2.4%) and 13 all-male bands (30.9%) are distributed in and around Jodhpur (Fig. 1). The total area used by these langurs comprises about 85 sq. km. There are no other langur troops found in a radius of 100 km around and thus the Jodhpur population is geographically and genetically isolated.

Water is available round the year for all the troops in the form of tanks, lakes and ponds. There are no natural predators except a few cases of dog predation (Agoramoorthy 1987). Religious people workship these langurs as God Hanuman (mentioned in the Hindu epic Ramayana), and provide them with artificial food regularly.

Study troops: The reproductive and troop demographic data presented here refer particularly to three one-male troops named B, KI and KII (Fig. 1).

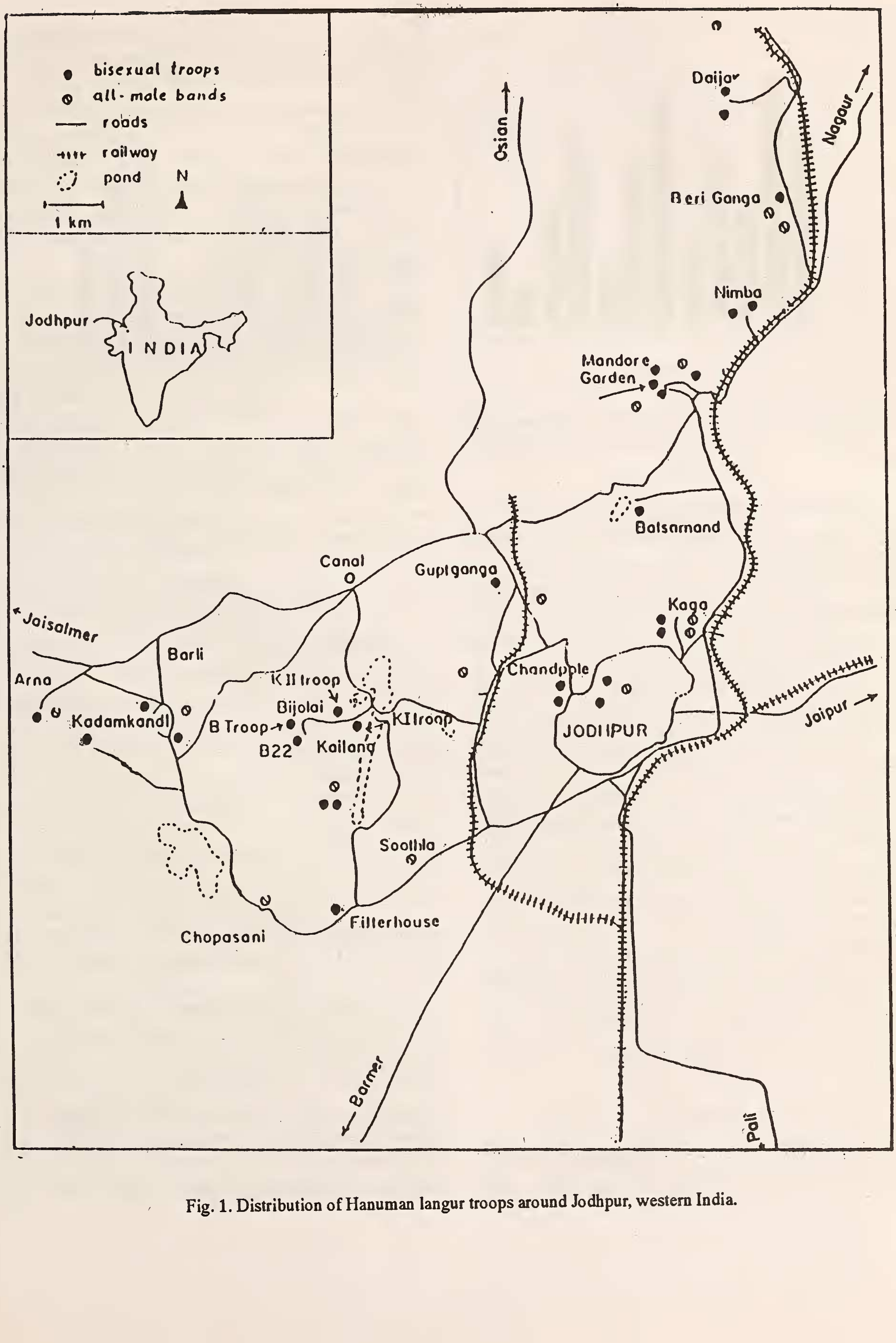

Fig. 1. Distribution of Hanuman langur troops around Jodhpur, western India.

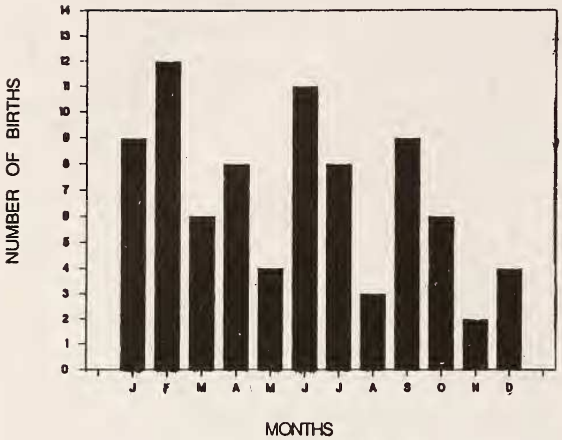

Fig. 2. Births observed during 1984 in 9 troops (2 multi-male, 7 one-male) of Hanuman langur, which are not influenced by infanticide.

Troop B or Bijolai troop: Troop B lives in Bijolai area and its home range overlaps that of neighbouring KII and B22 troops. Mohnot (1971) started to observe this troop in 1969 and was later followed by Makwana (1979), Winkler (1984) and Agoramoorthy (1987). All langurs of the troop were individually known since 1977.

Troops KI & KII (Kailana I & II): Prior to 1977, troops KI and KII were a single troop named B25 (Mohnot 1974). In 1977, fission occurred during a male band invasion into the troop (Winkler 1981). As a result, leader male of B25 continued its stay with 14 females, later named as troop KI. A new adult male along with eight females formed the second, named troop KII. Now troops KI and KII live in close proximity in Kailana area and their home ranges overlap. The past history of KI was published by Vogel and Loch (1984) and Winkler *et al.* (1984), whereas no earlier data was available on the individuals of troop KII. Individuals were identified and given names in July 1983, when I resumed regular observations.

Methods

The study troops were regularly observed from 10 December 1982 to 15 September 1985 for approximately 1850 hours to record the female reproductive parameters. All the individuals of the troops were checked every day to record new births, menstruation and sexual interactions with the leader male. As soon as a new born was seen, the last successful copulation date of the particular female was pooled out from reproductive records to estimate the length of gestation period. Ad libitum sampling was used as observational method (Altmann 1974).

Data on male band interactions with the focal troops and social changes like new male takeovers and infanticide were recorded. The influence of male takeover and infanticide in troop development was examined. To investigate birth seasonality in free ranging langurs around Jodhpur, nine bisexual troops (two multi-male and seven one-male troops) were followed once a week to record new births. Age of the infants was estimated based on colouration of face and coat (e.g. Mohnot 1974, Hrdy 1977).

Results

Female Reproductive Parameters

Births: Out of the total 41 infants that were born into the focal troops during 1982-85, one birth took place at dawn. When I resumed observation on 23 December 1983 at 0545 hrs, a new born infant was seen with the mother. The mother was in sitting posture, licking her infant. Fresh blood drops scattered around (15 cm radius) the place (over a rock) where the female was seen, indicated that the birth might have occurred about 30 minutes earlier. The infant was seen suckling with closed eyes. Six hours later, the infant was transferred to another female for about eight minutes. The vaginal bleeding lasted for four days.

In total, 17 infants were born in troop KII and 12 each in troop KI and B during the study period. Two distinct birth peaks were observed in this sample —a slow but steady increase in birth from January to March with a peak in March, and a sudden drop in April; and again a slow increase from May to July with another peak in July. This followed a gradual decrease in births, which were

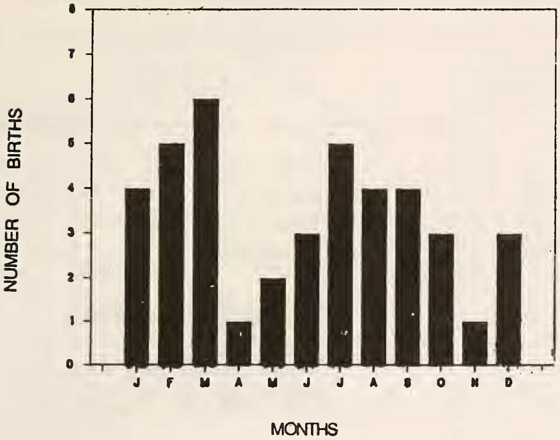

Fig. 3. Births observed in 3 troops (KI, KII and B) of Hanuman langur, which suffered infanticide during 1982-85.

lowest in November (Fig. 2).

In addition to this, nine bisexual troops (two multi-male and seven one-male troops) were followed in 1984 to record births and to investigate birth peak if any. Of 82 birth records, 48 were males and 34 were females. Births occurred in all the months in 1984. Although there was no distinct birth peak, fluctuations in the number of infants born in different months were observed. The concentration of births in January and February was evident compared to March and April, when fewer births were recorded. But in June and September there was again an increase in births while November was the lean month with minimum births. Likewise, August, May and December also had less births (Fig. 3).

Maturity: The onset of first menstruation was observed in two females at the age of 29.5 and 26 months and these females delivered their first infant after 5 and 7.7 months respectively. The first conception was estimated for five females at a mean age of 33.9 ± 3.2 months (range 30.3 to 37.2 months).

Menstruation: The successive menstrual bleeding in 35 cases for 10 females were recorded; it ranged from 16 to 31 days with an average of 24.8 ± 1.0 days. The bleeding lasted for 1-3 days (average 2 days) and in all cases blood flow was clearly visible.

Gestation: The time elapsed between last copulation and delivery of infant was calculated in 11 females and the gestation length ranged from 196 to 204 days (average 199.9 ± 3.0 days).

Birth interval: The time interval between two subsequent births was recorded for 24 cases in 18 females, whose infants were still alive when their younger siblings were conceived and born. This regular or normal birth interval ranged from 12.3 to 22.3 months and averaged 15.7± 2.4 months. The birth interval of females who lost their unweaned infants in eight cases ranged from 7.3 to 15.5 months, average 10.5 ± 2.9 months. It is significantly shorter than the normal birth interval (Mann-Whitney U Test, $P < 0.001$).

Troop Development

Considerable fluctuations in troop size and troop development were observed in the focal troops within the study period, mainly caused by births, deaths and disappearances of infants, juveniles and adults. After an extended process of male replacement and infanticide in troop KII, the troop structure changed considerably from 25 to 19 individuals (Table 3). In troop B, drastic changes in troop size from 21 to nine individuals was observed after male takeover (Table 4).

In both troops, infanticide was the major cause for infant and juvenile mortality. After the new males were established as leaders, both troops KII and B showed distinct increase in troop composition. In troop KI, there was not much fluctuation in the troop size since the troop did not suffer infanticide (Table 2). Details on the process of male replacement and social changes have been published elsewhere (Agoramoorthy 1987, Agoramoorthy and Mohnot 1988, Agoramoorthy *et al.* 1988).

Discussion

Although a few cases of diurnal births have been reported in Hanuman langur (McKenna 1974, Oppenheimer 1976), most of the births occurred at night. Many species of Cebidae and

TABLE 1
COMPARISON OF FIELD AND LABORATORY DATA ON FEMALE REPRODUCTIVE PARAMETERS OF *Presbytis entellus*

Female reproductive parameter	Published results	Field (F)/ Laboratory (L)	Source
Maturation			
Age at	28.2 m	Jodhpur (F)	Winkler *et al.* 1984
menarche	27.8 m	Jodhpur (F)	Present study
Age at first	34.2 m	Jodhpur (F)	Winkler *et al.* 1984
conception	36.4 ± 6.7 m	Jodhpur (F)	Present study
Menstruation			
Length of	26.8 ± 1.0 d	Jaipur (L)	David & Ramasamy 1969
menstrual	28 d	Mount Abu (F)	Hrdy 1977
cycles	24.1± 3.8 d	Jodhpur (F)	Winkler *et al.* 1984
	24.8 ± 1.0 d	Jodhpur (F)	Present study
Gestation			
Length of	172 d	Jaipur (L)	David & Ramasamy 1969
gestation	200 ± 10 d	Davis (L)	Neurater (pers. comm.)
period	6-7 m	Dharwar (F)	Sugiyama 1967
	200 ± 10 d	Mount Abu (F)	Hrdy 1974
	200.1 d	Jodhpur (F)	Winkler *et al.* 1984
	199.9 ± 3.0 d	Jodhpur (F)	Present study
Interbirth Interval			
Birth interval in	20-24 m	Dharwar (F)	Sugiyama 1967
normal cases	20-30 m	Mount Abu (F)	Cited in Harley 1985
	15.3 m	Jodhpur (F)	Winkler *et al.* 1984
	15.9 m	Berkeley (L)	Harley 1985
	15.7 ± 2.4 m	Jodhpur (F)	Present study
Birth interval in	25-27 m	Dharwar (F)	Sugiyama 1967
cases of infant loss	24 m	Mount Abu (F)	Hrdy 1977
	11.6 m	Jodhpur (F)	Winkler *et al.* 1984
	10.8 m	Berkeley (L)	Harley 1985
	10.5 ± 2.9 m	Jodhpur (F)	Present study

d = day, m = month

Cercopithidae tend to give birth at night (Jolly 1972). This would serve two functions (Bowden *et al.* 1967). First, the mother monkey has to move with the troop during the day in order to protect herself and if she is in the process of parturition, she will risk accidental predation by large carnivores in that area.

Second, in many species, adults are attracted and fascinated by new born infants and especially in Hanuman langurs, allo- mothering is very common, so it is presumably advantageous for langur females to deliver at night in order to safeguard their infants from inexperienced allo-mother interruption immediately after birth, who could damage the new born.

In the Himalayan population of langurs, distinct birth seasons occur. Births are spaced every 20-24 months and the seasonal breeding characters appear to be influenced by the high altitude habitat (Bishop 1979). In the non-Himalayan Hanuman langur population, births occur throughout the year without any seasonality but sometimes with clear birth peaks (Prakash 1962, Jay 1965, Sugiyama 1965, Hrdy 1977, Roonwal and Mohnot 1977, Bishop 1979).

However, there are always some out-of-season exceptions, and when coupled with small sample sizes these exceptions make the existence

TABLE 2
CHANGES IN THE GROUP COMPOSITION OF TROOP KI DURING JULY 1983-JUNE 1985

Date	Category & Sex		Langur I.D. No.	Event	Gain/ Loss	Troop Size
6 July '83	I	F	4.4.1	New birth	+ 1	18
7 Aug. '83	I	F	6.3.1	New birth	+ 1	19
23 Aug. '83	I	M	4.6	New birth	+ 1	20
9 Sep. '83	I	M	2.3.1	New birth	+ 1	21
? Sep. '83	A	F	9	Disappeared	− 1	20
23 Oct. '83	I	M	12.2	New birth	+ 1	21
13 Jun. '84	I	F	2.3.1	Died of electrocution	− 1	20
14 Jun. '84	A	F	8	Disappeared	− 1	19
25 Jul. '84	I	M	7.6	New birth	+ 1	20
24 Oct. '84	I	F	4.4.1	Disappeared	− 1	19
20 Jan. '85	I	M	6.3.2	New birth	+ 1	20
09 Feb. '85	I	F	4.4.2	New birth	+ 1	21
16 Mar. '85	I	F	3.2.1	New birth	+ 1	22
25 Mar. '85	I	M	12.3	New birth	+ 1	23
29 Mar. '85	I	M	7.6	Disappeared	− 1	22
08 Apr. '85	I	M	12.3	Died (reason not known)	− 1	21
08 Jun. '85	I	F	4.7	New birth	+ 1	22

A = Adult, I = Infant, M = Male, F = Female.
Group composition as on 1 July 1983 = 17 individuals.

of a real birth season questionable (cited in Moore 1985). There was no distinct birth peak for the nine troops which did not undergo male takeovers during 1984 and births were recorded throughout the year (Fig. 2). In contrast, the birth peak is convincing for the focal troops (Fig. 3). Here the sudden increase in number of births during February-March and July-September was a result of male replacements followed by infanticide in troops KII and B.

In Hanuman langurs, although the male juveniles started to wean from 14 to 18 months (Mohnot *et al.* 1987), the process of male maturity was difficult to observe, since male juveniles leave the natal troops during male replacements (Agoramoorthy 1987). The first menstrual cycle was observed in two cases and conception after 4-6 estrous cycles. In females who produced one or more infants, the conception normally occurred after two estrous cycles after postpartum. It appears that langur females reach their initial sexual maturity at the age of 2.5 to 3 years around Jodhpur. The mean age of females at first conception was estimated for six females as 36.4 months (Table 1).

Although in some study sites the flow of menstrual bleeding was not always detectable (Hrdy 1977, Jay 1965), in 35 subsequent menstrual cycles observed in 10 females in this study, the menstrual bleeding was clearly visible and the bleeding on average lasted for two days. The mean cycle length in the present study was 24.8 ± 1.0 days, which is closer to Winkler *et al.* (1984) (24.1 days) and David and Ramasami (1969) (26.8 ± 1.0 days) for captive colony langurs at Jaipur (Table 1). However, at Mount Abu, the average cycle length was 28 days (Hrdy 1977).

The normal birth interval of females whose infants survived at least for nine months averaged 15.7 months, which is closer to 15.4 months obtained from captive colony of langurs at Berkeley (Harley 1985). But the interval varied from 20-24 months for langurs of Dharwad (Sugiyama 1967) and 20 to 30 months for langurs of Mount Abu (Hrdy 1977, cited in Harley 1985). Six out of eight females that lost their unweaned infants under six months of age, conceived within two estrous periods after losing their infants, which is similar to the reports of Harley (1985). These six females started to deliver infants after 6.8 to 8.3 months

TABLE 3
CHANGES IN THE GROUP COMPOSITION OF TROOP KII DURING AUGUST 1983- SEPTEMBER 1985

Date	Category & Sex		Langur I.D. No.	Event	Gain/ Loss	Troop Size
23 Aug. '83	I	M	6.1	Attacked by invading male; infant disappeared next day	–1	24
12 Oct. '83	I	F	3.1	Attacked by invading band males, infant later disappeared	–1	23
15 Oct. '83	J	F	?	Died, reason not known	–1	22
20 Nov. '83	J	M	9.1	Attacked by invading male, later joined band (M 10)	–1	21
10 Dec. '83	I	F	?	Disappeared	–1	20
? Jan. '84	I	M	10.1	Disappeared, suspected infanticidal episode	–1	19
23 Feb. '84	I	F	5.1	New birth	+1	20
18 Mar. '84	I	M	4.2	New birth	+1	21
02 Apr. '84	I	F	5.1	Infanticide	–1	20
04 May '84	I	M	12.2	New birth	+1	21
11 May '84	I	M	12.2	Infanticide	–1	20
26 May '84	J	F	8.1	Died of electrocution	–1	19
06 Jun. '84	I	M	4.2	Infanticide	–1	18
11 Jun. '84	I	M	6.2	New birth	+1	19
16 Jun. '84	J	F	?	Died; dysentery and loss of body weight	–1	18
17 Jun. '84	I	M	6.2	Infanticide	–1	17
19 Jun. '84	I	M	9.2	New birth	+1	18
27 Jul. '84	I	M	1.1	New birth	+1	19
01 Aug. '84	I	M	11.2	New birth	+1	20
31 Aug. '84	I	M	10.2	New birth	+1	21
07 Sep. '84	I	F	7.1	New birth	+1	22
15 Sep. '84	I	F	8.2	New birth	+1	23
10 Nov. '84	I	M	5.2	New birth	+1	24
20 Dec. '84	I	M	12.3	New birth	+1	25
08 Jan. '85	I	M	4.3	New birth	+1	26
29 Apr. '85	I	M	4.1.1	New birth	+1	27
10 Aug. '85	I	M	11.3	New birth	+1	28
25 Aug.'85	I	F	8.2	Died of electrocution	–1	27
26 Sep. '85	I	F	6.3	New birth	+1	28

J = Juvenile, I = Infant, M = Male, F = Female.
Group composition as on 1 Aug. 1983 = 25 individuals.

and the birth interval averaged nine months, which is very close to the birth interval of females who suffered abortion and still birth at Berkeley colony (Harley 1985, p. 232).

In the remaining two females, who were older (approximately 12 years), conception took place after four and nine months respectively. The female who lost the youngest infant had the longest birth interval of 15.5 months. In particular, this female lost her second infant subsequently in infanticide, which appeared to be the reason. Does older age play a key role in lengthening birth interval in females who lose infants ? Do females adopt any strategy to prolong the birth interval in order to avoid losing their infant in infanticide? More data are required to test this hypothesis.

Comparing the age of infant at death or disappearance, with the duration of birth interval in females who lose their infants, after excluding the extreme two cases, a positive correlation was

TABLE 4
CHANGES IN THE GROUP COMPOSITION OF TROOP B DURING JANUARY 1983 - JULY 1985

Date	Category & Sex		Langur I.D. No.	Event	Gain/ Loss	Troop Size
12 Jan. '83	J	M	7.3	Disappeared	–1	20
17 Jan. '83	A	M	M. Star	Attacked and killed by invading males	–1	19
17 Jan. '83	A	F	3	Died, reason not known	–1	18
17 Jan. '83	A	M	M 38	Joined as new leader	+1	19
18 Jan. '83	J	M	3.5	Disappeared	–1	18
18 Jan. '83	J	M	Cripple	Disappeared	–1	17
18 Jan. '83	J	F	?	Disappeared after new male takeover	–1	16
30 Jan. '83	J	F	7.4	Died due to infection from bite wounds	–1	15
01 Feb. '83	A	F	7	Died; intestinal parasite *Strongyloides* sp. found during examination	–1	14
03 Feb. '83	I	M	5.4	Infanticide	–1	13
09 Feb. '83	I	F	6.5	Infanticide	–1	12
11 Feb. '83	I	M	1.5	Infanticide	–1	11
11 Feb. '83	A	F	5	Isolation, starvation and eventual disappearance after she lost her infant	–1	10
13 Feb. '83	A	F	9	Dog predation	–1	09
07 Oct. '83	I	M	1.6	New birth	+1	10
22 Oct. '83	I	M	1.6	Disappeared, reason not known	–1	09
23 Dec. '83	I	F	6.6	New birth	+1	10
25 Jan. '84	I	M	2.7	New birth	+1	11
20 Feb. '84	I	M	6.1.3	New birth	+1	12
29 Feb. '84	I	M	2.4.1	New birth	+1	13
02 July '84	I	M	1.7	New birth	+1	14
08 Mar. '85	I	M	6.7	New birth	+1	15
23 Mar. '85	I	M	6.1.4	New birth	+1	16
01 Jul. '85	I	F	6.4.1	New birth	+1	17

A = Adult, J = Juvenile, I = Infant, M = Male, F = Female.
Group composition as on 1 Jan. 1983 = 21 individuals.

found (Fig. 4). This indicates that the dominant male langur, who newly takes over a bisexual troop, will gain reproductive advantage if he successfully kills unweaned infants under six months of age (supposedly unrelated), in order to bring the mother into early estrous to sire his own offspring. He can thus increase his inclusive fitness (Trivers 1972, Hrdy 1977). But this advantage may vary depending upon the biological condition of the females.

Drastic decline in troop size was observed in troops B and KII as a result of male takeovers and infanticide. The highest infant mortality (87.5%) was observed in troop KII. In addition, three juveniles (two males and one female) disappeared in troop B after male change. But in one case, a male juvenile of troop KII was attacked and later joined a neighbouring band of males. This indicates that juvenile stage in males is critical since they are forced to leave their natal troop during male takeovers and have to face a new life with the bachelor males. But whether the reason for the disappearance of a female juvenile was due to emigration, predation, or other causes, is unknown.

It is evident that the male replacements strongly influenced troop structural changes in Hanuman langurs of Jodhpur. This is similar to

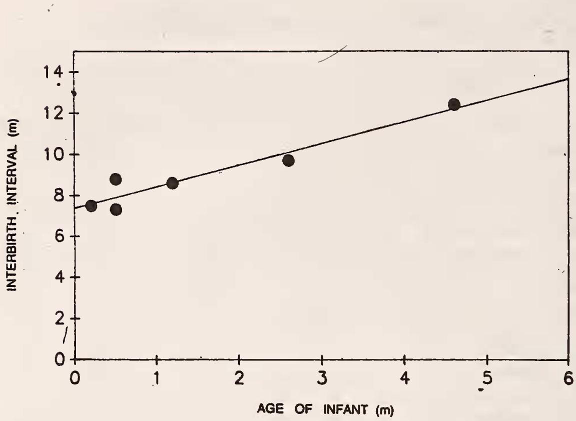

Fig. 4. A positive correlation between the age of infants at death and duration of interbirth interval in Hanuman langurs of Jodhpur.

the phenomenon in purplefaced langurs *Presbytis senex* and in lions *Panthera leo,* where increased infant mortality during male takeovers has been reported (Rudran 1973, Bertram 1975, Packer and Pusey 1983).

Langurs around Jodhpur appear to reach maturity about one year earlier than at other study sites like Dharwar and Mount Abu (Vogel and Loch 1984), and in addition the interbirth interval is comparatively shorter (Table 1). However, Harley (1985) compared the langur reproductive data of Jodhpur to the langurs of Mount Abu and Dharwar and argued that Mount Abu and Dharwar results were overestimated since these data did not result from long-term observations like Jodhpur, so inaccuracy on langur parturition and undetected loss of pregnancy or neonate seemed to be the cause for overestimation.

It is clear that the long-term langur reproductive data from Jodhpur and Berkeley colony are similar. Here, I must mention that Jodhpur habitat is semi-desert and natural food appears to be scarce (Agoramoorthy 1987). In addition, artificial food is common to all langur troops around Jodhpur. But, how far the artificial provisioning will affect the birth interval in langurs of Jodhpur is not clear. Studies on Japanese macaques showed that artificial food reduced birth interval in females (Sugiyama and Ohsawa 1985). More detailed and longer-term data are needed from other study sites such as Dharwar and Mount Abu to better examine the effect of artificial food in shortening birth interval in langurs, and also to note the difference in reproductive parameters within the species *Presbytis entellus* itself.

Acknowledgements

I thank Drs. S.M. Mohnot and R. Rudran for their advice and supervision during the course of the field and writing work. The field work was supported by a Senior Research Fellowship from the Government of India, Department of Environment (Man & Biosphere Program) and data analysis and writing work was funded by the Friends of the National Zoo (FONZ) and David and Lucile Packard Foundation (grant awarded to Dr R. Rudran). I also thank the Department of Zoology, University of Jodhpur and the Conservation & Research Center, Smithsonian Institution for providing facilities. I wish to express my thanks to Drs S.M. Mohnot, R. Rudran, N.H. Bishop, J. Moore, C. Wemmer, and Ms. Minna Hsu for critically reading the manuscript of an earlier version.

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